

# FEEDING MECHANISM OF THE ECHIUROID, *OCHETOSTOMA* *ERYTHROGRAMMON* LEUCKART & RUEPPELL, 1828

S. H. CHUANG

*Dept. of Zoology, University of Singapore, Singapore*

The feeding mechanism of both *Urechis caupo* and *Echiurus echiurus* has been described. The former (Fisher and MacGinitie, 1928) secreted a mucus tube 2–8 inches long, the open upper end of which was fastened to the burrow near its opening, while the lower end remained attached to the body. This tube filtered the water flowing through the burrow, became loaded with food particles and was subsequently swallowed. *Echiurus echiurus* fed intermittently in aquaria (Gislén, 1940). Periods of feeding of 1–2 days alternated with rest periods lasting several days. During each feeding period food collection occurred at intervals of 20 minutes to a couple of hours. The proboscis emerged from the burrow in feeding, as Wilson (1900) had previously noted, with its distal margin facing anteriorly and dorsally towards the substratum to gather food particles and transfer them to the ventral surface where they were glued together with mucus and carried by ciliary currents towards the mouth.

The feeding mechanism of *Ochetostoma* is unknown, except for the observation of Sluiter (1884) that in the shallow water-covered part of the beach at Billiton the proboscides of *O. erythrogrammon* moved slowly on the sand to shovel up sand and organic matter on to the proboscis groove and convey them to the mouth.

In the present study observations were made on *Ochetostoma* specimens both in their natural habitat on the beach and also in the laboratory.

## MATERIALS AND METHODS

*Ochetostoma erythrogrammon* occurs in large colonies between mean low water neaps and mean low water springs in the intertidal sandy mud of Singapore and neighboring islands. An opening, 3 mm. in diameter, through which the proboscis may emerge in feeding, leads into a U-shaped burrow of 1 cm. diameter. The burrow consists of two vertical or oblique tunnels each 20 cm. long connected by a horizontal tunnel 25–45 cm. long. Although the burrows can be located by the proboscides above the surface at ebb tide, digging up the animals without damage is not easy because of the difficulty of locating the direction of the horizontal tunnel due to blocking up of the other opening of the burrow by a plug of sand or mud.

Sluiter (1884) reported the ease with which the intact animal was obtained by pressing the foraging proboscis on the sand with the fingers and digging up the trunk with the other hand at Billiton. Due presumably to the less muddy substratum around Singapore, this method always resulted in autotomy.

Aquaria were set up by using sandy mud from the same bed from where the specimens were collected. Fine carborundum powder was used to trace the ciliary currents on the proboscis under the binocular microscope.

## RESULTS AND DISCUSSION

At Pulau Hantu, a sandy island south of Singapore, which rises one meter above the highest spring tide, the substratum from mid-tide level downwards consists of greyish to purplish impervious clay with an overlying layer of coarse muddy sand 2-5 cm. thick. At ebb tide the water retained in the interstices of the sand at the higher shore levels slowly drains along and thus wets the sandy crust above the clay subsoil of the lower shore. At every ebb tide, irrespective of the time of day or night, *Ochetostoma erythrogrammon* feeds by extending its proboscis out of the burrow with the dorsal surface touching the substratum to collect sand and detritus with the dorsally turned distal region of its proboscis. When the surface sand and detritus near the mouth of the burrow are taken up, the proboscis extends further in approximately the same direction. The fully extended proboscis, exceeding 25 cm. in length in some specimens, becomes thin and narrow. Its entire ventral surface is covered with sand grains, detritus and extruded mucus (Fig. 1).



FIGURE 1. *Ochetostoma erythrogrammon*. The proboscis, stretched horizontally across figure and loaded with sand and detritus, forages on the wet sand outside the burrow (arrow) at ebb tide. Tracks on sand above burrow indicate previous excursions of proboscis.

The smaller particles move towards the mouth along the length of the proboscis but the larger sand grains seem to remain stationary until muscular contractions of adjacent parts of the proboscis move them on. When poked with a stick the fully extended proboscis withdraws, discarding the collected sand grains and detritus at the mouth of the burrow. After an interval of time the proboscis re-emerges to extend in a different direction from the one previously taken. At the end of the low tide several tracks indicating foraging excursions of the proboscis may be seen radiating from the opening of the burrow (Fig. 1).

On more than ten visits to Pulau Hantu during ebb tide proboscides of *Ochetostoma* foraging on the wet sand were observed. That the same specimens protruded their proboscides at every ebb tide is demonstrated by the following observations. During ebb tide at 3:30 A.M. on 27th August 1961 the burrows through which

19 proboscides protruded were marked by iron rods driven into the clay near the opening of the burrow. During the next ebb tide at 5:45 P.M. on the same day 8 proboscides emerged from the marked burrows to forage in brilliant sunshine. They returned into the burrows when rising tide flooded the openings. This method of feeding occurs only when the surface sand is wet enough, since it also occurs on the wet muddy shore of the west coast of Singapore Island, but not on the crumbly, porous, well-drained muddy sand of an adjacent island where a bed of *Ochetostoma* is also found. Stephen and Robertson (1952) also reported the presence of tracks radiating from one side of the opening of *Ochetostoma* burrow on the sandy shore at Mbweni, Zanzibar.

The proboscis underwent frequent changes of shape. It rolled itself up into an almost closed cylinder by apposition of the lateral margins. It flattened out into a long thin ribbon during feeding. It shortened to less than a fifth of the length of the fully contracted trunk or extended to more than four times the length of the relaxed trunk. The width varied between 3 and 11 mm. Observations under the binocular microscope showed that the ventral surface changed frequently from a plane to a concave shape. Moreover, longitudinal troughs and transverse grooves on the ventral surface and puckers along the lateral margins appeared and disappeared in various regions according to the degree of contraction of the underlying muscles.

The cilia lined only the ventral surface of the proboscis and were of uniform length of 11–13  $\mu$  in the living state, unlike those of *Echiurus echiurus*, in the proboscis of which Gislén (1940) reported larger cilia on the tip, lateral margins and the "eminence."

As regards the ciliary currents the ventral surface of the proboscis can be subdivided into three regions, namely the distal, middle and proximal regions. The distal region had in its distal 4 mm. or so only posteriorly directed ciliary currents. These also occurred in the middle of its proximal 4 mm., where they were flanked by postero-medially directed ciliary currents (Fig. 2a). During feeding the extremely mobile distal region turned dorsally to explore the substratum and pick up particulate matter. It was also used for digging a burrow.

The middle region, which formed the greater part of the proboscis and varied in length with the degree of extension, had medially directed ciliary currents along the lateral fields. There were posteriorly directed ciliary currents in the middle flanked by postero-medially directed ciliary currents (Fig. 2b).

The proximal region, almost as mobile as the distal region, had a tract of posteriorly directed ciliary currents along the middle. This tract was flanked by a narrow tract of postero-medially directed ciliary currents. Lateral to this was a tract of medially directed ciliary currents. In addition to these there were several narrow tracts of cilia beating laterally outwards along the thickened rim. The rim on each side puckered up into folds and valleys. By referring to the pigments on the rim it was possible to observe that the folds and valleys were not fixed in position but could vary. The valleys at any particular moment could become folds at the next. As a result of this arrangement the movement of particulate matter along the rim could be outward or inward according to whether the outwardly beating or the inwardly beating tracts of cilia were oriented at the top of the fold.

In the laboratory an intact specimen extended its proboscis 4–7 cm. with the

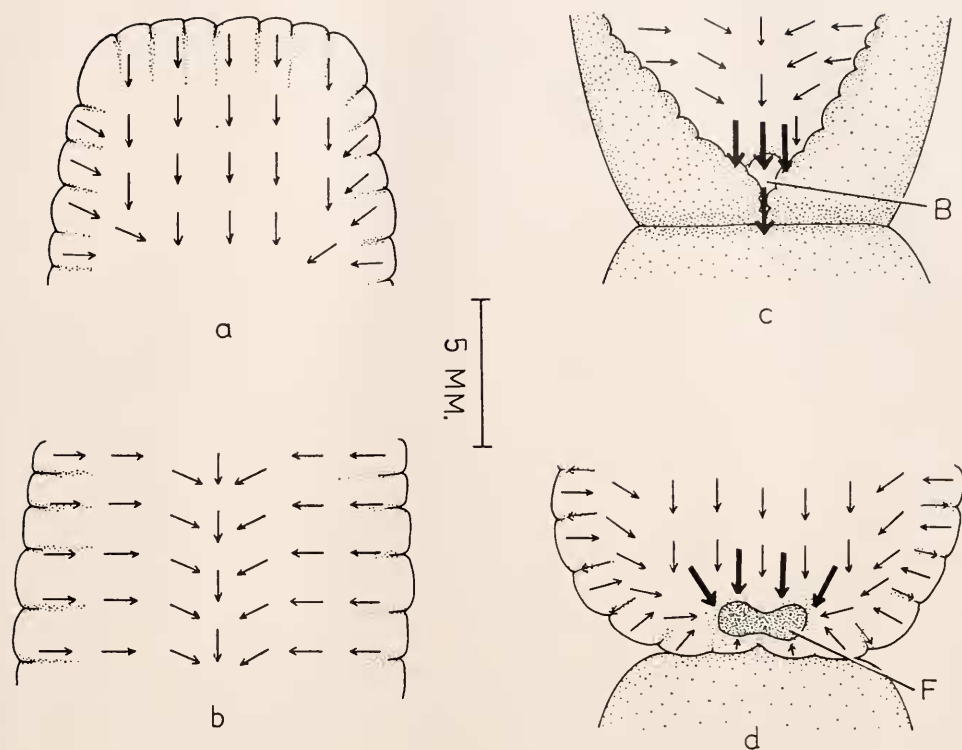


FIGURE 2. Ciliary currents (small arrows) and paths (large arrows) of accepted and rejected particles on the proboscis of *Ochetostoma erythrogrammon*. a and b, ventral view of distal and middle regions, respectively. c, ventral view of proximal region rejecting particles; B = bulge. d, antero-ventral view of proximal region accepting particles into the mouth funnel (F).

dorsal surface touching the bottom of the waxed tray. The distal part of the proboscis swung from side to side and its ventral surface faced dorsally to scour the substratum and pick up particles of carborundum added. These were coated with mucus and carried in the median tract of posteriorly directed ciliary currents through the expanded proximal region into the mouth (Fig. 2d). When particles of clean sand 1 mm. or more in diameter approached the proximal region, this soon partially rolled up into a cylinder and became dorso-ventrally depressed. A bulge also formed 2-3 mm. anterior to the mouth. The passage into the funnel-shaped proximal region was thus blocked. These large particles therefore moved posteriorly across or alongside the anterior part of the bulge, over the rim of the proboscis ventrally (Fig. 2c) and were rejected.

The equivalent of the bulge of *Ochetostoma* in *Echiurus echiurus* is presumably the ridge or "eminence," since Gislén (1940) found that it could bulge or sink into a furrow. He believed that the peristaltic movements of the eminence helped to move the mucus thread down the mouth-funnel. Two ventral lips or swellings of the proximal region of the proboscis fitted into the depressions on either side of



the eminence to prevent larger particles from entering the mouth in *Echiurus echiurus*. In this and in *Ochetostoma erythrogrammon* the rejection mechanism is therefore muscular and differs only in small details. Fisher and MacGinitie (1928) observed that large particles were rejected when the mucus tube was being swallowed by *Urechis caupo* but the details of this rejection mechanism were not described.

Intact specimens placed in aquaria with muddy-sand bottom built U-shaped tunnels by forcing the distal region of the proboscis into the sand and working out a hole with it while the trunk meantime lay prostrate on its side or dorsal surface. The proboscis disappeared into the hole dragging the trunk after it as in *Urechis caupo* (Fisher and MacGinitie, 1928). The ventral setae were not used in digging the hole in *Ochetostoma*. In *Urechis* they were used in enlarging the tunnel by scraping off material from the sides (Fisher and MacGinitie, 1928). *Echiurus echiurus*, however, performed digging movements alternately with the ventral setae at the rate of 6–9 times per minute and the stiffened anterior end of the trunk, while the proboscis remained inactive. Gislén (1940) found that the anterior end of the trunk entered the excavated hole dragging the proboscis along, and illustrated (text-figure 10 at page 15) the posterior end of the trunk and the distal tip of the proboscis remaining outside at one stage of digging a burrow. In spite of the closer systematic relationship between *Ochetostoma* and *Echiurus*, the former resembled more closely the more distant relative *Urechis caupo* in its digging behavior.

When the surface of the aquarium substratum was under 3–4 cm. of water, the proboscis in *Ochetostoma* remained inside the burrow and performed feeding movements by exploring and picking up particles along the wall of the burrow with the distal region of the proboscis. After some time the animal turned around so that the proboscis could explore and collect particles from the other end of the burrow. *Echiurus* also put out part of its proboscis while still submerged under water to collect food particles of the aquarium bottom (Wilson, 1900; Gislén, 1940) and leave distinct tracks (Gislén, 1940). Some time after the water in the aquarium was siphoned out, *Ochetostoma* extended its proboscis out of the burrow to feed in the same manner as observed under natural conditions on the beach. The collection of food particles with the proboscis inside or outside the burrow is presumably the usual method of feeding in all echiuroids, since *Urechis caupo* also gathered sediment with its proboscis while lying outside the burrow in an aquarium (Fisher, 1946). Due to the reduced size of the proboscis in *Urechis caupo*, an alternative method involving filtration of food particles with mucus tube was developed. No mucus tube of the type secreted by *Urechis caupo* was formed in *Ochetostoma*.

#### SUMMARY

1. *Ochetostoma erythrogrammon* built U-shaped burrows between mean low water neaps and mean low water springs in the intertidal sandy mud of Singapore and neighboring islands.
2. At ebb tide the proboscis emerged from the burrow in wet beaches to collect and swallow sand grains and detritus from the surface of the shore.
3. The ciliary currents on the proboscis and the course of the accepted and rejected particles were described.

4. The feeding mechanism of *Ochetostoma erythrogrammon* was compared with those of *Echiurus echiurus* and *Urechis caupo*.

## LITERATURE CITED

- FISHER, W. K., 1946. Echiuroid worms of the North Pacific Ocean. *Proc. U. S. Nat. Mus.*, **96**: 215-292.
- FISHER, W. K., AND G. E. MACGINITIE, 1928. The natural history of an echiuroid worm. *Ann. Mag. Nat. Hist., Ser. 10*, **1**: 204-213.
- GISLÉN, T., 1940. Investigations on the ecology of *Echiurus*. *Lunds Univ. Årsskr., new ser.*, **36**: 1-39.
- SLUTTER, C. P., 1884. Beitræge zu der Kenntnis der Gephyreen aus dem malayischen Archipel, 3. Mittheil. *Natuurk. Tijdschr. Ned.-Ind.*, **43**: 26-88.
- STEPHEN, A. C., AND J. D. ROBERTSON, 1952. A preliminary report on the Echiuridae and Sipunculidae of Zanzibar. *Proc. Roy. Soc. Edinb., Sect. B*, **64**: 426-440.
- WILSON, C. B., 1900. Our North American echiurids. *Biol. Bull.*, **1**: 163-178.